
PHYLOGENETIC RELATIONSHIPS BETWEEN *HOYA* AND THE MONOTYPIC GENERA *MADANGIA*, *ABSOLMSIA*, AND *MICHOLITZIA* (APOCYNACEAE, MARSDENIEAE): INSIGHTS FROM FLOWER MORPHOLOGY¹

Livia Wanntorp^{2,3} and Paul I. Forster¹

ABSTRACT

The monotypic genera *Absolmsia* Kuntze, *Madangia* P. I. Forst., Liddle & I. M. Liddle, and *Micholitzia* N. E. Br. (Apocynaceae, Marsdenieae) are, according to molecular phylogenetic results, nested within the genus *Hoya* R. Br. Together with *Dischidia* R. Br., these genera are considered to comprise a well-supported clade within the tribe Marsdenieae. Flower morphology of *Absolmsia*, *Madangia*, and *Micholitzia* is examined by SEM and light microscopy and compared to that of the related *H. caudata* Hook. f., *H. curtisii* King & Gamble, *H. hypolasia* Schltr., *H. lacunosa* Blume, *H. patella* Schltr., *H. retusa* Dalzell, and *H. venusta* Schltr. We discuss the morphological evidence that supports the reduction of these genera into *Hoya*. Among characters supporting such a position is the presence of a pellucid margin on the pollinia of *Absolmsia*, *Madangia*, *Micholitzia*, and *Hoya* that is absent on the pollinia of *Dischidia*. *Absolmsia* and *Madangia* have a staminal corona with outer and inner lobes, similar to that of *Hoya*. While the outer corona processes of *Absolmsia* and *Micholitzia* are free and revolute, as in most species of *Hoya*, those of *Madangia* are laterally fused forming a continuous skirt resembling the corona of certain species of *Hoya*. The flowers of *Micholitzia* are superficially similar to those of *Dischidia* in its urceolate corolla, but the staminal corona with revolute outer processes decidedly links *Micholitzia* to *Hoya*. The new combination *H. inflata* (P. I. Forst., Liddle & I. M. Liddle) L. Wanntorp & P. I. Forst. is proposed. For *Micholitzia obcordata* N. E. Br., the name *H. yuennanensis* Hand.-Mazz. has nomenclatural priority and should therefore be used when including *M. obcordata* in *Hoya*.

Key words: *Absolmsia*, Apocynaceae, corolla, corona, *Dischidia*, *Hoya*, *Madangia*, Marsdenieae, *Micholitzia*, morphology, pellucid margin, phylogeny, pollinaria, pollinia.

The tribe Marsdenieae Benth (1868) (Apocynaceae, Asclepiadoideae) is thought to include 29 genera and over 570 species distributed in the New and the Old Worlds (Omlor, 1998). The taxonomic positions of the genera *Cionura* Griseb., *Dregea* E. Mey., *Dischidia* R. Br., *Gymnema* R. Br., *Hoya* R. Br., *Marsdenia* R. Br., *Micholitzia* N. E. Br., *Rhyssolobium* E. Mey., *Stephanotis* Thou., and *Telosma* Coville have been examined in previous morphological and molecular phylogenetic studies (Liede & Albers, 1994; Forster, 1995; Endress & Bruyns, 2000; Potgieter & Albert, 2001; Sennblad & Bremer, 2002; Rapini et al., 2003; Livshultz, 2003; Meve & Liede, 2004; Wanntorp et al., 2006a). However, only a few species of each of these genera were included in

these studies, leaving several relationships within the Marsdenieae unresolved.

One of the genera in the Marsdenieae whose taxonomic delimitations remain unclear is *Hoya*, the wax plants of ornamental horticulture, a large tropical genus of over 300 herbaceous to succulent species of which about 40 are commonly found in cultivation (Forster et al., 1998, 1999, 2002), although many more are cultivated in specialist collections. Species of *Hoya* are distributed from mainland Asia (China, India, Vietnam, Burma, Laos, Cambodia) through Malaysia, Indonesia, and New Guinea to Australia and the western Pacific islands (Forster & Liddle, 1996). Most species of *Hoya* are laticiferous wiry climbers, often epiphytic, with fleshy to succulent leaves of

¹ We thank Prof. S. S. Renner (Ludwig Maximilians University, Munich) for supporting the laboratory work of this study; A. Boström, C. Forsberg-Heikkilä, D. J. Liddle, and T. Nyhuus for sharing flower material; E. Facher, M. Vasyka, and A. Kocyan (Ludwig Maximilians University, Munich) for laboratory assistance; and D. Goyder (Royal Botanic Gardens, Kew) for kind help with the herbarium specimen of *Hoya spartioides*. This paper is part of a research project by the first author supported by the Swedish Research Council.

² Ludwig Maximilians University Munich, Institute of Systematic Botany, Menzinger Strasse 67 D-80638 Munich, Germany.

³ Correspondence and current address: Department of Botany, Stockholm University, Lilla Frescativ. 5, SE-10691 Stockholm, Sweden livia.wanntorp@botan.su.se.

¹ Queensland Herbarium, Environmental Protection Agency, Brisbane Botanic Gardens, Mt. Coot-tha Road, Toowong Qld 4066, Australia.

various size, color, and venation. A minority of species are non-climbing and with foliage that is either erect or pendent. The sympetalous flowers are clustered in umbelliform extra-axillary inflorescences mostly with perennial peduncles (Forster et al., 1998). The complex, fleshy flowers of *Hoya* comprise a pentamerous corolla that is highly variable in shape, color, and dimensions; a staminal corona with inner processes adnate to the anther connective and outer processes with revolute lobes; a gynostegium, standing on a short or long column above the corolla and including five fused anthers, the ovaries, and the style head (Forster et al., 1998); and two pollinia from adjacent anthers, united by a translator apparatus secreted from the style head to a pollinarium (Omlor, 1998; Kleijn & van Donkelaar, 2001).

A morphological revision of the Marsdenieae placed *Hoya*, *Dischidia*, and the monotypic genera *Absolmsia* Kuntze, *Madangia* P. I. Forst., Liddle & I. M. Liddle, and *Micholitzia* together in a *Hoya*-group, sharing an epiphytic habit, fleshy to succulent leaves (in *Absolmsia* only present at an early age stage), generally persistent extra-axillary inflorescences, and comose and fusiform seeds without prominent wings but with keel-shaped thickenings on the seed coats (Omlor, 1998; Livshultz, 2003). In addition to Omlor's work, a possible close relationship between *Micholitzia*, *Madangia*, *Absolmsia*, and *Hoya* was discussed in morphological papers specific to each of these genera (Goyder & Kent, 1994; Forster et al., 1997; Kloppenburg, 2001). While the first two of these studies discussed the similarity of *Madangia inflata* P. I. Forst., Liddle & I. M. Liddle and *Micholitzia obcordata* N. E. Br. to *Hoya* without taking position regarding the relationship of these species to *Hoya*, Kloppenburg (2001) concluded that *A. spartioides* Kuntze should be included in *Hoya* based on its morphological similarities in the corolla and corona. Kloppenburg therefore proposed a change of name for the single species of *Absolmsia* to *H. spartioides* (Benth.) Kloppenb. None of these studies, however, examined relationships using a phylogenetic approach. Another species has been referred to the genus *Absolmsia*, namely *A. oligophylla*. This taxon was, however, recently shown to belong to the genus *Tylophora* R. Br. (Gilbert et al., 1995).

Recently, two molecular phylogenetic studies based on chloroplast gene regions of the *trnL* intron, *trnL-trnF* spacer, and *atpB-rbcL* spacer, as well as on nuclear sequences of the ribosomal ITS region, were conducted to examine the phylogeny of *Hoya* and its taxonomic delimitation (Wanntorp et al., 2006a, b). Thirty-five species of *Hoya*, three species of *Dischidia*, *Absolmsia spartioides*, *Madangia inflata*, and *Micholitzia obcordata* were analyzed, together with

species representing subfamilies Periplocoideae and Secamonoideae, as well as tribes Fockeae, Marsdenieae, Ceropegieae, and Asclepiadeae (sensu Endress & Stevens, 2001; Verhoeven et al., 2003). A major result of these studies was that *Hoya* is paraphyletic without the inclusion of the monotypic genera *Absolmsia*, *Madangia*, and *Micholitzia*, which are all found clearly nested among the 35 species of *Hoya* examined (Wanntorp et al., 2006a, b).

The aim of the present study is to examine the flower morphology of *Absolmsia spartioides*, *Madangia inflata*, *Micholitzia obcordata*, and a selection of closely related species of *Hoya* by using light and SEM microscopy. We discuss which morphological characters bear on the phylogenetic and taxonomic positions of these genera within *Hoya*.

MATERIAL AND METHODS

We examined the floral morphology of the species *Absolmsia spartioides*, *Hoya caudata* Hook. f., *H. curtisii* King & Gamble, *H. hypolasia* Schltr., *H. lacunosa* Blume, *H. patella* Schltr., *H. retusa* Dalzell, *H. venusta* Schltr., *Madangia inflata*, and *Micholitzia obcordata*. Flower material at anthesis was collected and stored in 70% ethanol at the Botanical Department of Stockholm University, except for the material of *Madangia inflata* provided by D. J. Liddle (Queensland, Australia), of *Absolmsia spartioides* by T. Nyhuus (Järfälla, Sweden), of *H. curtisii* by A. Boström (Stockholm, Sweden), and of *H. hypolasia* and *H. venusta* by C. Forsberg-Heikkilä (Porvoo, Finland). The identity of all species examined was confirmed with the literature or by comparison with original type material. Table 1 reports voucher information for the specimens examined.

SEM and light microscopic studies were performed on all species mentioned above with the exception of *Hoya hypolasia* and *H. venusta*, which were only examined by SEM microscopy, due to scarce material. For SEM microscopy, all flowers were dehydrated in an alcohol-acetone series, critical-point dried, and sputter-coated with gold. SEM microscopy was done with a LEO 438 VP scanning electron microscope (Zeiss, Jena, Germany) at the Department of Systematic Botany, Ludwig Maximilians University, Munich. For sectioning, microtome sections were made using 2-hydroxyethyl methacrylate embedding (Igersheim & Cichocki, 1996), cut at 10 µm, and stained with toluidine blue and ruthenium red. When discussing the morphology of a single corona lobe, we use the term corona lobe, while we define the inner and outer parts of each lobe by using the terms inner (ip) and outer (op) processes, respectively.

Table 1. Voucher information on the specimens used in the present study. Herbarium abbreviations follow Index Herbariorum (Holmgren et al., 1990).

Species	Voucher information
<i>Absolmsia spartioides</i> Kuntze	Wanntorp L. 592 (S), Sipitang, Borneo
<i>Hoya caudata</i> Hook. f.	Wanntorp L. 593 (S), ex hort. Department of Botany, Stockholm University
<i>Hoya curtisii</i> King & Gamble	Wanntorp L. 597 (S), ex hort.
<i>Hoya hypolasia</i> Schltr.	Wanntorp L. 594 (S), ex hort.
<i>Hoya lacunosa</i> Blume	Wanntorp L. 571 (S), ex hort. Department of Botany, Stockholm University
<i>Hoya patella</i> Schltr.	Wanntorp L. 575 (S), ex hort. Department of Botany, Stockholm University
<i>Hoya retusa</i> Dalzell	Wanntorp L. 580 (S), 1998–3127, Rosendal Uppsala, Uppsala Botanical Garden
<i>Hoya venusta</i> Schltr.	Wanntorp L. 595 (S), ex hort.
<i>Madangia inflata</i> P. I. Forst., Liddle & I. M. Liddle	D. J. Liddle IML 1076 (BRI), Madang Province, New Guinea
<i>Micholitzia obcordata</i> N. E. Br.	Wanntorp L. 596 (S), ex hort.

RESULTS

1. *Hoya spartioides* (Benth.) Kloppenb., *Fraterna* 14: 8. 2001. Basionym: *Astrostemma spartioides* Benth. in Hook., *Ic. Pl.* 14: 7. 1880. *Absolmsia spartioides* (Benth.) Kuntze, as “*spartioides*,” *Revis. Gen. Pl.* 2: 418. 1891. TYPE: [Malaysia]. North Borneo, s.d., *Burbidge s.n.* (lectotype, designated here, K [1 of 2 (fl), 2 of 2 (st)] not seen).

Hoya spartioides is an epiphytic, sparsely branched, non-twining subshrub with fleshy leaves from Borneo. Inflorescences pedunculate, comprising concave umbels with 4 to 6 flowers; pedicels ca. 1 mm long, glabrous, rough. Calyx lobes obtuse-triangular, ca. 0.02 × 0.02 mm. Corolla shortly campanulate to salver-shaped, orange-yellow, glabrous, ca. 10 mm diam., with 5 triangular oval lobes, ca. 3 × 3 mm (Fig. 1A). Gynostegium on a short hairy column (Fig. 1C). Corona flat, star-shaped, white, smooth, covered by thick hairs on the upright part (Fig. 1A–C, E, G); inner processes of lobes narrow, spatulate, appressed to the anther appendages (Fig. 1D); outer lobes with deeply revolute processes (Fig. 1D, E); anther appendages lanceolate-acute, approximately as long as the corona lobes (Fig. 1F, G); style head flat (Fig. 1H). Pollinarium consisting of 2 pollinia connected by thickened winged caudicles to a corpusculum; pollinia square in outline, almost as long as wide, ca. 0.3 × 0.2 mm (Fig. 2E, G, H), the pellucid margin very wide but covering only ca. 1/3 of the dorsal margin of the pollinia (Fig. 2H); corpusculum thick, almost round in shape, ca. 0.2 × 0.2 mm, ending with 2 long, spreading appendages, upper part enclosing the caudicles, ca. 0.2 × 0.1 mm (Fig. 2F).

The herbarium specimen chosen as lectotype for *Hoya spartioides* was selected among the collections available for this plant at the Royal Botanic Gardens, Kew (D. Goyder, pers. comm., 2007).

2. *Hoya caudata* Hook. f., *Fl. Brit. Ind.* 4(10): 60. 1883. TYPE: [Malaysia]. “Malacca,” *Maingay 1128* (holotype, K not seen).

Hoya caudata is an epiphytic twiner with leathery-fleshy leaves from the Malay Peninsula and Thailand. Inflorescences pedunculate, comprising geotropic, concave umbels, with up to 12 pendent flowers; pedicels longer in the periphery of the inflorescence and shorter in its middle, 2–3 cm long, hirsute. Calyx lobes linear-lanceolate, ca. 2 × ca. 1 mm, glabrous. Corolla flattened-campanulate, pink-yellow, inside pubescent in the middle, with long caudate hairs at the margins (Fig. 3A, B), ca. 2 cm diam.; lobes ovate-triangular, acute-cuspidate, 4–7 × 4–5 mm (Fig. 3A). Gynostegium stalked on a short column (Fig. 3A). Corona with a dark red ring in the middle but lighter at the margins, smooth; inner processes slightly pointing up (Fig. 3C); outer processes very wide, bending upward, not deeply revolute (Fig. 3C); anther appendages slender and whip-like, very much exceeding the corona lobes (Fig. 3B–D); style head long-apiculate (Fig. 3D). Pollinarium comprising 2 pollinia connected by broadly winged and flattened caudicles to a corpusculum (Fig. 3E); pollinia longer than wide, cylindrical-elongate, ca. 0.8 × 0.2 mm; pellucid margin covering the dorsal margin of the pollinia; corpusculum narrow-rhomboid, ca. 0.2 × 0.1 mm, ending with 2 long, spreading appendages (Fig. 3F); caudicles ca. 0.1 × 0.1 mm (Fig. 3E).

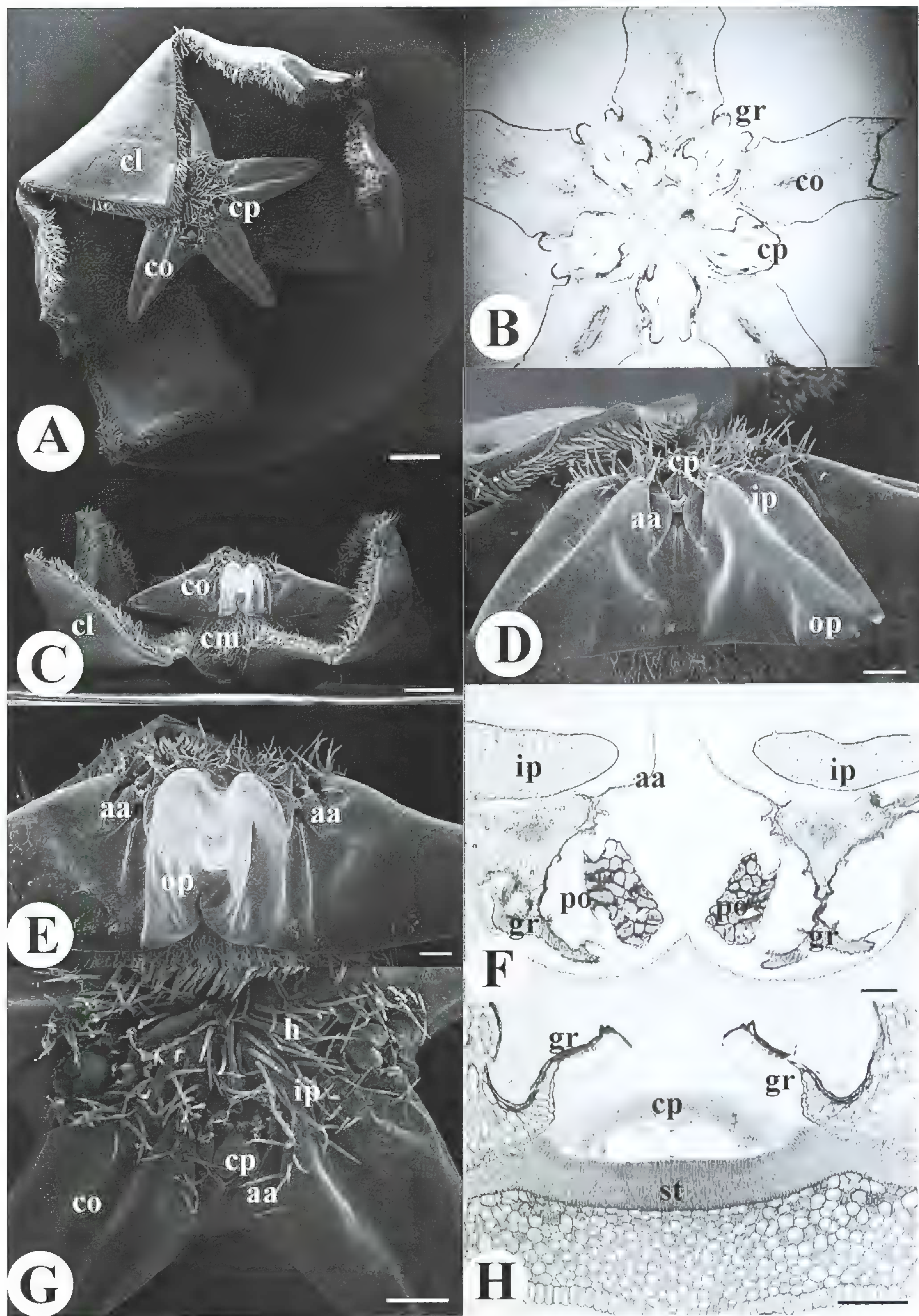


Figure 1. *Hoya spartioides*. —A, B. Top views of flowers showing remains of the corolla (cl), corona (co), guide rail (gr), and corpusculum (cp). —C. Side view of flower showing column (cm). —D, E. Details of coronas showing inner processes (ip), outer processes (op), anther appendages (aa), and corpusculum (cp). —F. Longitudinal section of flower showing the position of inner corona processes (ip), guide rail (gr), pollinia (po), and anther appendages (aa). —G. Detail of flower (top view) with corona (co) with hairs (h), anther appendages (aa), and corpusculum (cp). —H. Light micrographic section (longitudinal view) of flower showing the style head (st) and part of the corpusculum (cp). Scale bars = 1 mm (A, C), 4 mm (B), 100 μ m (F, H), 200 μ m (E), 300 μ m (D, G).

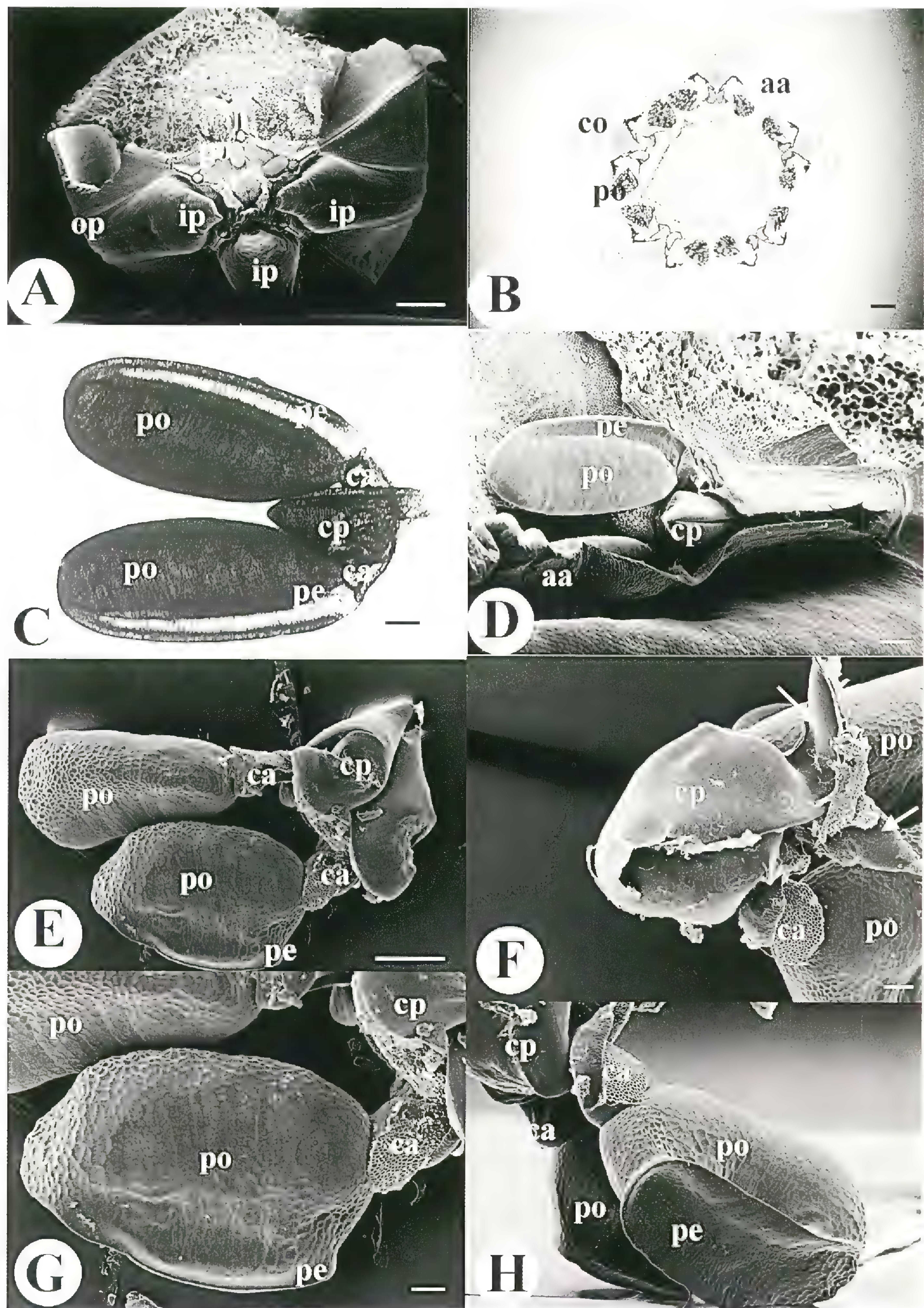


Figure 2. *Hoya inflata*. —A. Upper part of flower seen from above with inner (ip) and outer (op) corona processes, pollinia (po), and style head (st). —B. Cross section of flower showing the positions of coronas (co), anther appendages (aa), and pollinia (po). —C, D. Pollinaria with corpusculum (cp), caudicles (ca), and pollinia (po) with pellucid margins (pe) and one anther appendage (aa). Scale bars = 1 mm (A), 1 mm (B), 100 μm (C, D). *Hoya spartioides*. —E, G. Side view of pollinaria formed by the corpuscula (cp), the caudicles (ca), and the pollinia (po) with pellucid margin (pe). —F. Pollinarium seen from below. Arrows denote long appendages from the corpusculum partly covering the winged caudicles. —H. Pollinia (po) with broad pellucid margin (pe) and caudicles (ca). Scale bars = 30 μm (F–H), 100 μm (E).

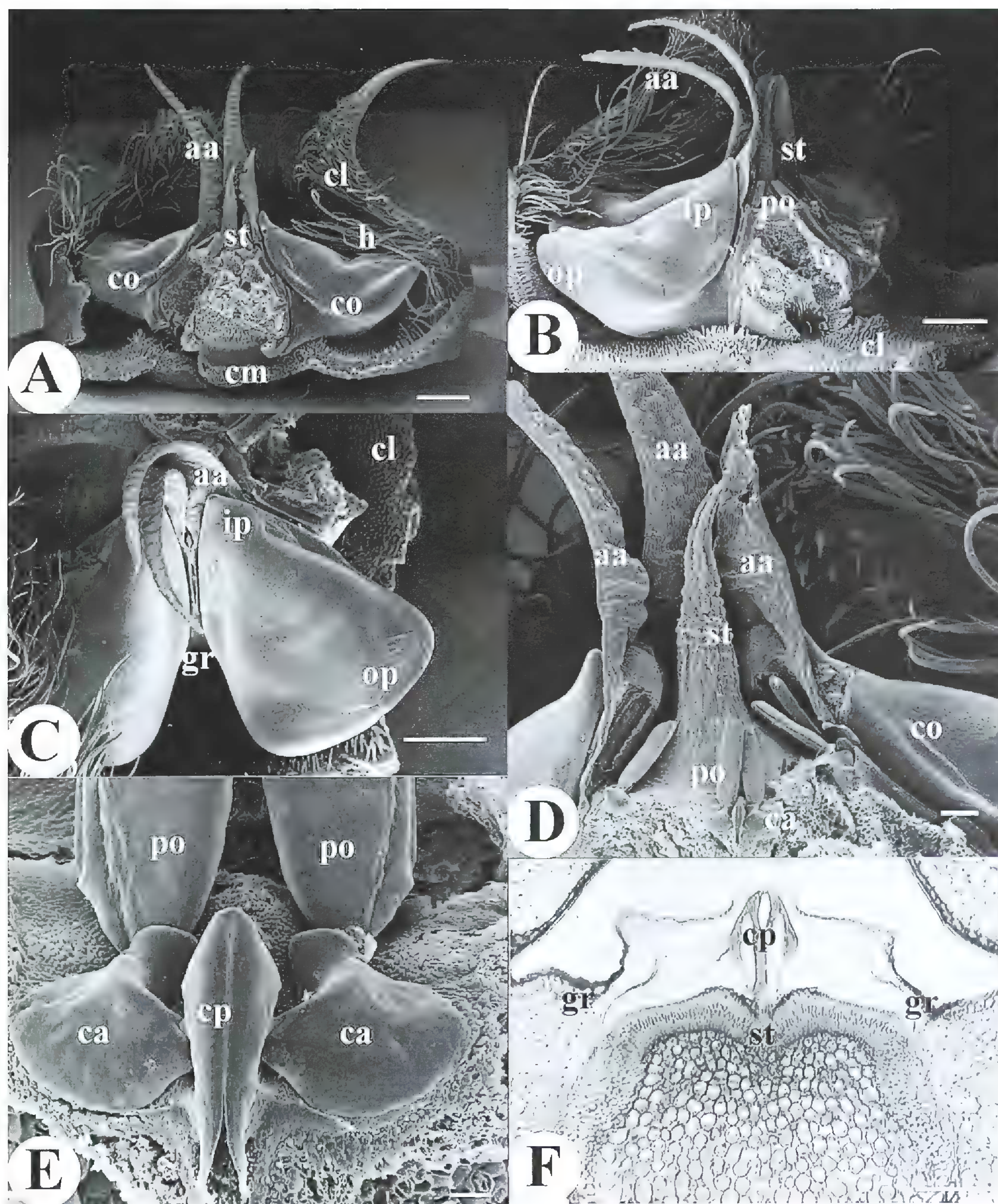


Figure 3. *Hoya caudata*. —A, B. Flowers showing remains of corolla (cl) with hairs (h), corona (co) with inner (ip) and outer (op) processes on a column (cm), anther appendages (aa), and style head (st). —C. Detail of flower showing guide rails (gr). —D. Upper part of flower with anther appendages (aa), style head (st), and pollinia (po) with falcate caudicles (ca). —E. Details of a pollinarium: pollinia (po), caudicles (ca), and corpusculum (cp). —F. Detail of flower showing the positions of guide rails (gr), corpusculum (cp), and style head (st). Scale bars = 1 mm (A–C), 200 μ m (D), 30 μ m (E), 100 μ m (F).

3. *Hoya curtisii* King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(2): 563. 1907. TYPE: Malay Peninsula, *Curtis 2894* (holotype, SING!).

Hoya curtisii is an epiphyte with non-twining pendent stems and succulent leaves from the Malay Peninsula. Inflorescences pedunculate, comprising convex, globose umbels with up to 30 flowers; pedicels ca. 22 mm long, densely hairy. Calyx lobes

narrowly triangular, ca. 2×1 mm. Corolla rotate, creamy white, inside completely pubescent, except on the margins, ca. 0.7 mm diam. (Fig. 4A); lobes oblong-ob lanceolate, acute at the tips, reflexed, ca. 7×4 mm. Gynostegium borne on an annular structure (annulus) on a high column (Fig. 4A, B, D). Corona red in the middle and white at the margins; lobes sulcate, with a central depression or an umbo (Fig. 4A); inner processes blunt (Fig. 4E); outer

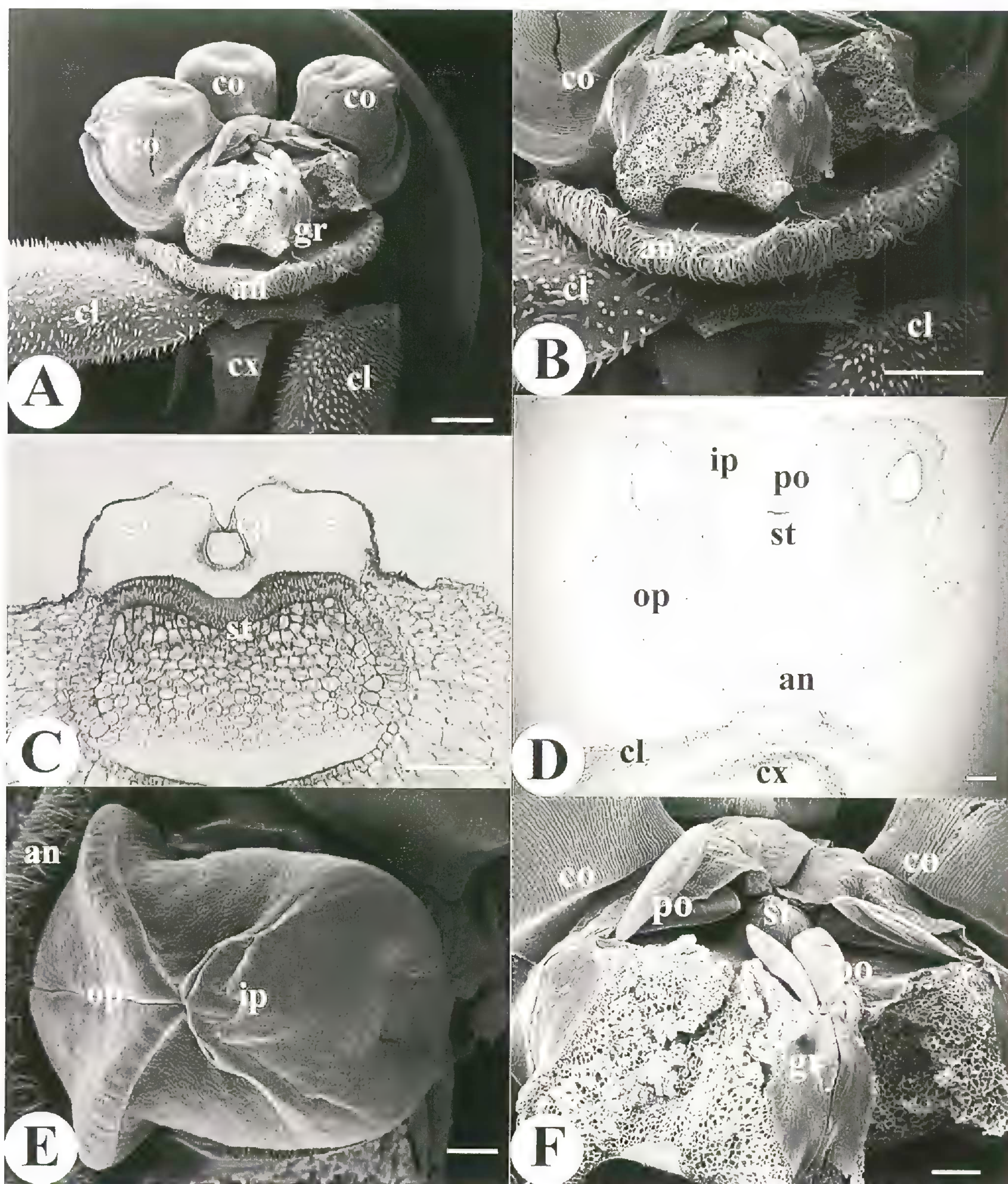


Figure 1. *Hoya curtisi*. —A, D. Flowers with calyx (cx), corolla (cl), corona (co) with inner (ip) and outer (op) processes, annulus (an), guide rails (gr), style head (st), and pollinia (po). —B. Enlargement of A showing the position of the annulus (an). —C. Part of flower showing guide rails (gr), corpusculum (cp), and style head (st). —E. Single corona lobe lying on annulus (an) with inner (ip) and outer (op) processes. —F. Part of flower showing coronas (co), guide rails (gr), pollinia (po), and style head (st). Scale bars = 1 mm (A, B), 2.8 mm (D), 100 μ m (C), 300 μ m (E, F).

processes made of 3 parts, of which 2 wide and bent against each other, and the third part bending upon these 2 and touching them (Fig. 4E); anther appendages lanceolate, blunt, exceeding the corona lobes (Fig. 5C); style head flat (Figs. 4C, F, 5C). Pollinarium comprising 2 pollinia attached by flattened and winged caudicles to a corpusculum; pollinia spindle-shaped, much longer than wide, ca. 10×0.3 mm (Figs. 4F, 5A, B, D); pellucid margin covering 1/2 of the dorsal margin of the pollinia (Fig. 5D); corpuscu-

lum ca. 1×0.3 mm, ending with 2 long, spreading appendages; caudicles ca. 0.1×0.04 mm (Fig. 5A, D).

4. *Hoya hypolasia* Schltr., Bot. Jahrb. Syst. 50: 123. 1913. TYPE: New Guinea. R. Schlechter 18075 (holotype, B not seen).

Hoya hypolasia is an epiphytic twiner with fleshy leaves from New Guinea. Inflorescences pedunculate,

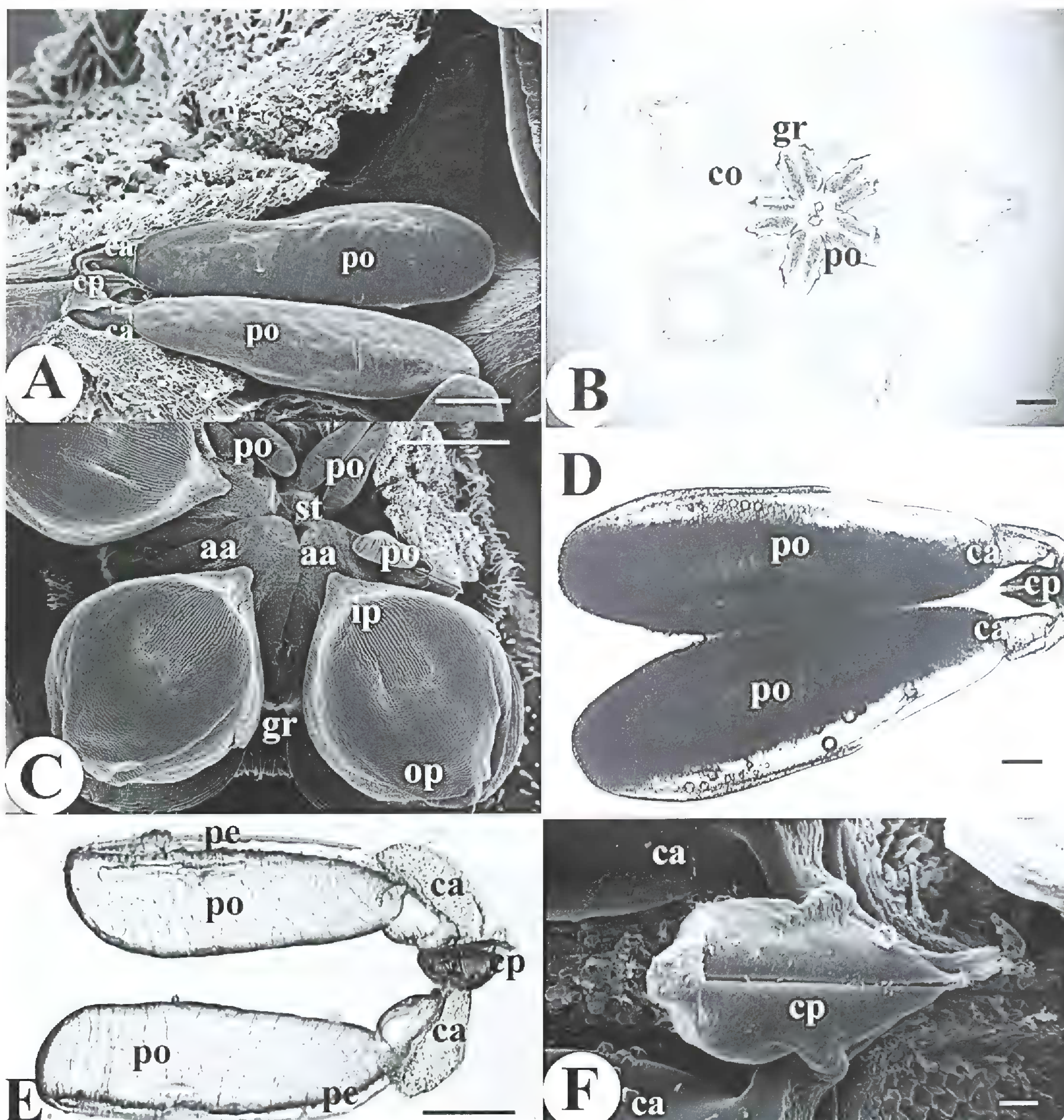


Figure 5. *Hoya curtisii*. —A, D. Pollinaria with pollinia (po), corpuscula (cp), and caudicles (ca). —B, C. Flowers (B, cross section), showing inner (ip) and outer (op) corona (co) processes, anther appendages (aa), guide rails (gr), pollinia (po), and style head (st). Scale bars = 1 mm (C), 2 mm (B), 100 μ m (D), 200 μ m (A). *Hoya lacunosa* —E. Pollinarium with corpusculum (cp), winged caudicles (ca), and pollinia (po) with pellucid margins (pe). —F. Detail of a pollinarium with corpusculum (cp) and part of caudicles (ca). Scale bars = 10 μ m (F), 100 μ m (E).

comprising concave umbels of ca. 10 flowers, ca. 2 cm diam.; pedicels ca. 40 mm long, glabrous. Calyx lobes obtuse, ca. 0.1 $\times$ 0.1 mm. Corolla flattened-campanulate, creamy white, outside glabrous, inside hairy, ca. 1.5 cm diam. (Fig. 6A, B, D); lobes ovate-triangular, ca. 0.8 $\times$ 0.6 mm. Inner processes of corona lobe very short and obtuse (Fig. 6F, H), not covering the anther appendages and the style head (Fig. 6C); outer processes revolute (Fig. 6F, H); anther appendages lanceolate, acute, exceeding the corona lobes (Fig. 6F); style head flat (Fig. 6C, D). Pollinarium

comprising 2 pollinia attached by broadly winged and flattened caudicles to a corpusculum; pollinia oblong-elongate, basal part protruding outward, ca. 0.9 $\times$ 0.3 mm (Fig. 6E, G); pellucid margin covering the entire dorsal margin (Fig. 6G); corpusculum ca. 0.2 $\times$ 1 mm, ending with 2 short appendages (Fig. 6G); caudicles very short, ca. 0.1 $\times$ 0.03 mm (Fig. 6E, G).

5. *Hoya lacunosa* Blume, Bijdr. Fl. Ned. Ind. 16: 1063. 1826. *Otostemma lacunosum* (Blume)

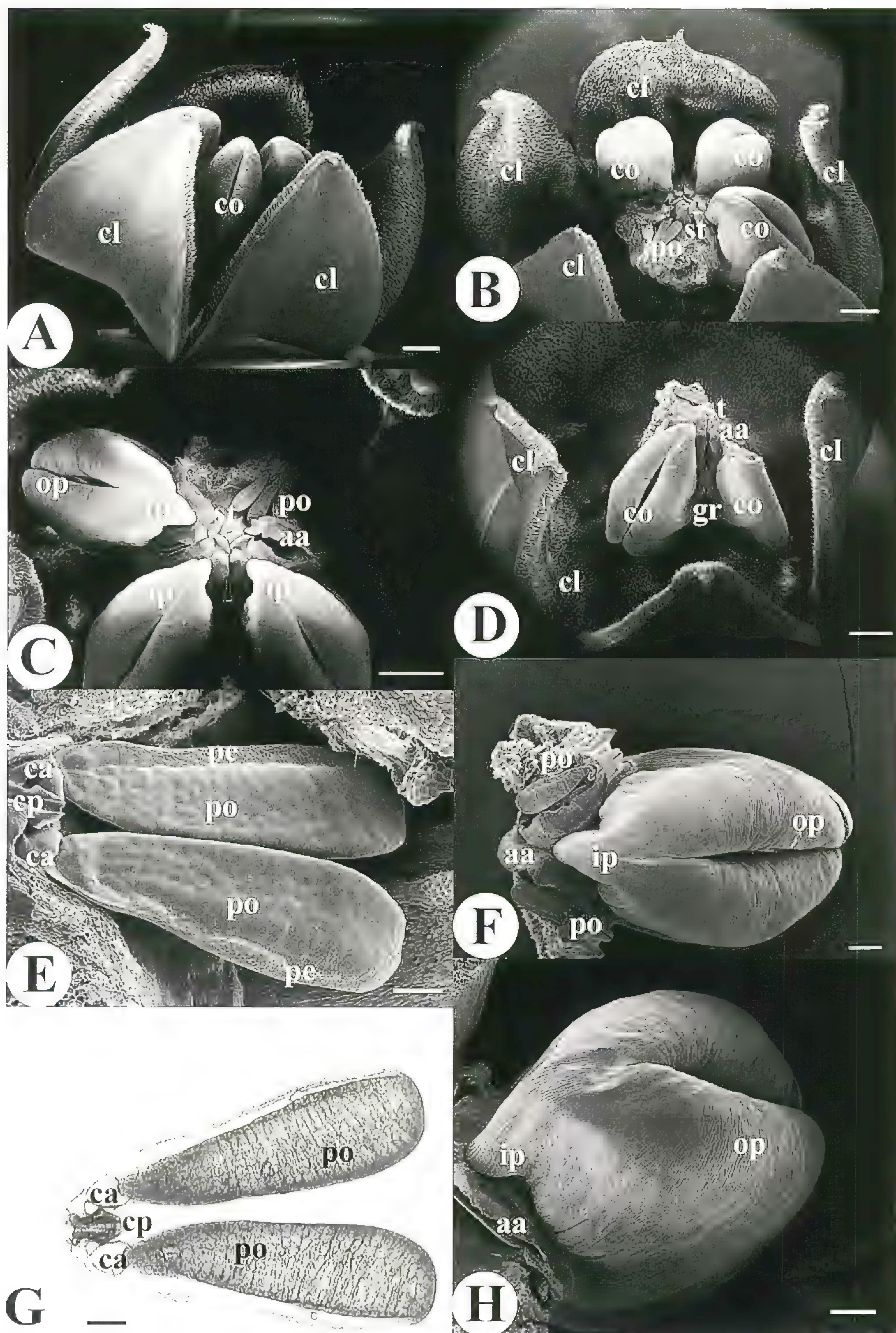


Figure 6. *Hoya hypolasia*. —A. Flower from side showing corollas (cl) and corona (co). —B–D. Parts of flowers seen from above with corolla (cl), inner (ip) and outer (op) corona (co) processes, guide rails (gr), anther appendages (aa), pollinia (po), and style head (st). —E, G. Pollinaria with pollinia (po), corpuscula (cp), caudicles (ca), and pollinia (po) with pellucid margins (pe). —F, H. Different views of single corona lobe with inner (ip) and outer (op) processes, anther appendages (aa), and pollinia (po). Scale bars = 1 mm (A–D), 100 μ m (E, G), 300 μ m (F, H).

Blume in Rumphia 4: 30. 1849. TYPE: Indonesia. *Horsfield s.n.* (holotype, K not seen).

Hoya lacunosa is a twiner from Thailand and the Malay Peninsula. Inflorescences pedunculate, comprising pendent, convex umbels, with up to 30 flowers, ca. 5 mm diam.; pedicels of outer flowers longer than central ones, 10–20 mm long, glabrous. Calyx lobes triangular, ca. 1×0.5 mm. Corolla rotate, white, ca. 5 mm diam.; lobes lanceolate, acute-cuspidate, totally reflexed giving the flower a globose shape, very hairy, ca. 4×2 mm (Fig. 7A). Gynostegium on a conspicuous column (Fig. 7G). Corona lobes elliptical, basal part forming a continuous structure looking like a skirt (Fig. 7B, D, F, G); inner processes acutely ascending, outer processes obtuse, slightly ascending (Fig. 7A–F); anther appendages lanceolate, acute, exceeding the corona lobes (Fig. 7F); style head shortly apiculate (Fig. 7E, H). Pollinarium comprising 2 pollinia attached by broadly winged and flattened caudicles to a corpusculum; pollinia elongate-falcate, ca. 0.4×0.1 mm (Fig. 5E); corpusculum ca. 0.1×0.1 mm, ending with 2 short appendages (Fig. 5E, F); caudicles thick, broadly winged, ca. 0.1×0.1 mm (Fig. 5E).

6. *Hoya inflata* (P. I. Forst., Liddle & I. M. Liddle) L. Wanntorp & P. I. Forst., comb. nov. Basionym: *Madangia inflata* P. I. Forst., Liddle & I. M. Liddle, *Austrobaileya* 5: 54. 1997. TYPE: Papua New Guinea, Madang Province: Headwaters Dom River, 26 Nov. 1995, I. M. Liddle IML1076 (holotype, BRI!).

Hoya inflata is an epiphytic twiner with fleshy leaves from New Guinea. Inflorescences pedunculate, comprising pendent, convex umbel, with up to 9 flowers, ca. 1×2 cm; pedicels sparsely hirsute, 30–45 mm long. Calyx lobes triangular, ca. 1×2 mm. Corolla urceolate-globose, fleshy, creamy white, basally hiding the calyx (Fig. 8D), glabrous on the outside, basal inside part covered by long, slender, woolly hairs, ca. 1×2 cm (Fig. 8A); lobes triangular, somewhat reflexed, ca. 5×6 mm. Gynostegium on a conspicuous hairy columnar structure (Fig. 8A). Corona made of 5 continuous lobes forming a membranous smooth skirt, whose lower part builds up a continuous rim that is bent inward (Fig. 8A, C–E), white; lobes free at the style head (Figs. 8E, F, 2A); anther appendages lanceolate, acute, protruding above the corona lobes (Fig. 8B, E); style head flat (Fig. 8B, F, G). Pollinarium comprising 2 pollinia connected by unwinged and flattened caudicles to a corpusculum; pollinia with oblong-round apical part, ca. 0.7×0.3 mm (Figs. 8G, 2B–D); pellucid margin covering the entire dorsal margin

of the pollinia and slightly protruding outward at the basal part; corpusculum oblong-ovate, ca. 0.4×0.2 mm (Fig. 2C, D); caudicles ca. 0.1×0.7 mm (Fig. 2C).

7. *Hoya yuennanensis* Hand.-Mazz., Symb. Sin. 7(4): 1001. 1936. TYPE: China, Yunnan: betw. Ota-Tanschan & Tsedjrong, 4 Oct. 1915, *Handel-Mazzetti* 7971 (holotype, W not seen).

Micholitzia obcordata N. E. Br., Bull. Misc. Inform. Kew 358. 1909. Syn. nov., non *Hoya obcordata* Hook. f., Fl. Brit. India 4: 56. 1885. *Dischidia obcordata* (N. E. Br.) J. F. Maxwell & R. van Donkelaar, Nat. Hist. Bull. Siam. Soc. 39: 78. 1991. TYPE: “India & Burma,” cult. Royal Bot. Gard. Glasnevin, Dublin, 1909, *Micholitz s.n.* (holotype, K not seen).

Hoya lantsangensis Tsiang & P. T. Li, Acta Phytotax. Sin. 12: 126. 1974. Syn. nov. *Antiostelma lantsangense* (Tsiang & P. T. Li) P. T. Li, Novon 2: 218. 1992. TYPE: China, Yunnan: Mo-Jiang, Talang, A. Henry 13589 [cited by Tsiang & P. T. Li as A. Henry 13689] (holotype, NY not seen; isotypes, IBSC not seen, K not seen).

Hoya manipurensis Deb, J. Indian Bot. Soc. 34: 50. 1955. *Antiostelma manipurense* (Deb) P. T. Li, Novon 2: 219. 1992. TYPE: India, Manipur: Litan, 1 Sep. 1953, D. B. Deb 1081 (holotype, CAL not seen).

Hoya yuennanensis is an epiphytic vine with fleshy leaves from China (Yunnan), India, Burma, and Thailand. Inflorescences pedunculate, comprising racemes of up to 7 flowers, ca. 1.4×0.8 mm; pedicels ca. 2 mm long, hirsute. Calyx lobes obtuse-triangular, ca. 0.2×0.3 mm, slightly pubescent. Corolla narrowly urceolate, greenish with reddish lobular margins uniformly densely pilose on the outside; tube wider at the base and gradually narrowing up to the rim, inside covered by uniformly distributed long hairs, ca. 1.2×0.6 mm (Fig. 9A); lobes triangular, slightly reflexed, inside densely pilose, ca. 0.2×0.1 mm (Fig. 9A). Corona with 5 fleshy sulcate lobes, white; inner processes short and slightly bent upward (Fig. 9C); outer processes with a deep groove (Fig. 9C, D); anther appendages much exceeding the corona lobes and ending with a triangular structure that touches the style head (Fig. 9A–C, E); style head short, conical. Pollinarium comprising 2 pollinia connected by flattened, unwinged caudicles to a corpusculum; pollinia lying in an almost horizontal position in regard to the corona, almost squared, ca. 0.2×0.2 mm (Fig. 9F, G); pellucid margin covering the entire dorsal margin of the pollinia (Fig. 9F, G); corpusculum rhomboid, ca.

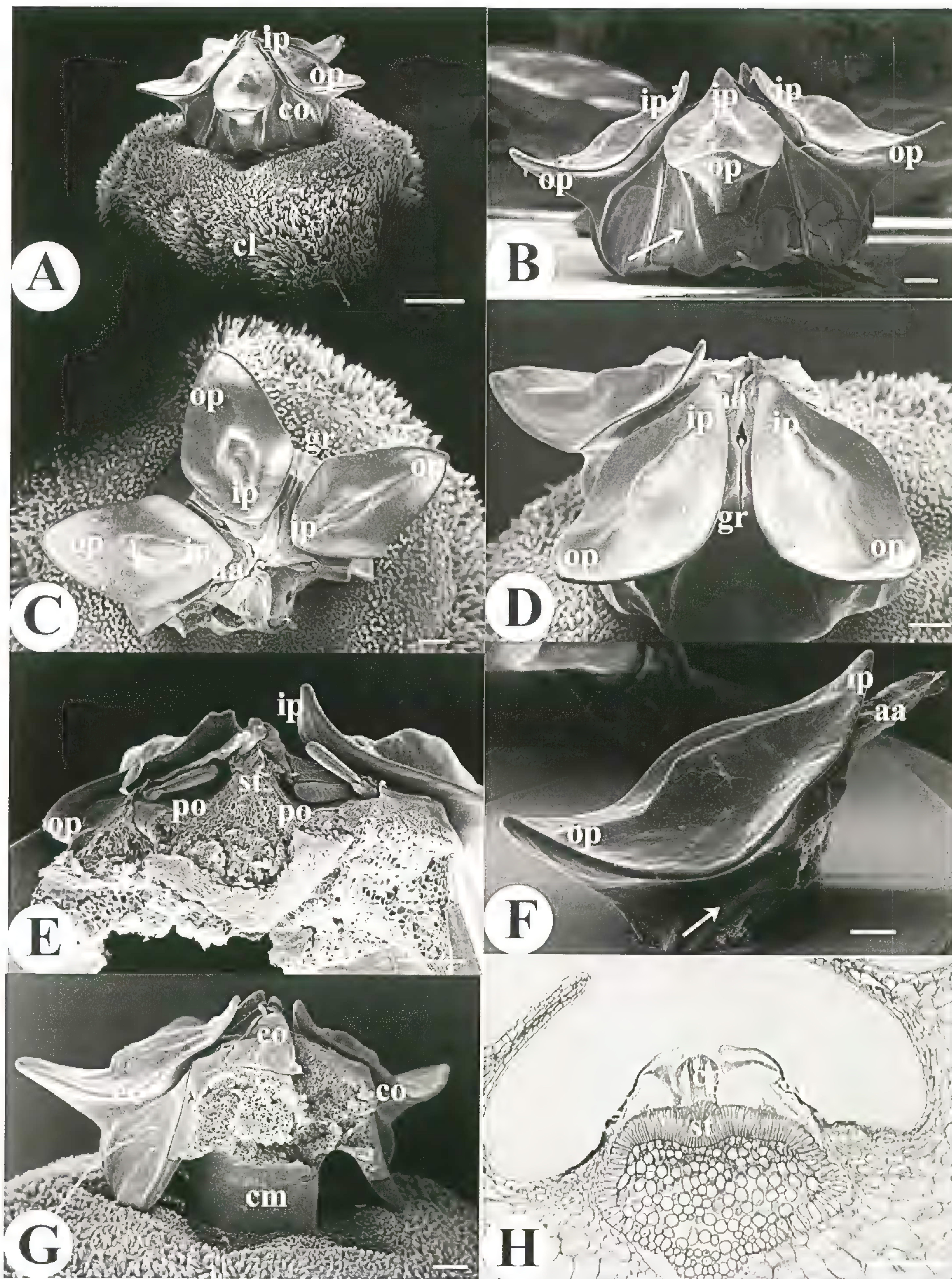


Figure 7. *Hoya lacunosa*. —A. Flower with corolla (cl) and inner (ip) and outer (op) corona (co) processes. —B–D. Different views of coronas with inner (ip) and outer (op) processes, anther appendages (aa), and guide rails (gr). Arrow shows the fused outer corona processes. —E. Section of flower showing pollinia (po) and style head (st). —F. Single corona lobe with inner (ip) and outer (op) processes and adnate anther appendage (aa). Arrow shows the fused outer corona processes. —G. Corona (co) seen from side showing column (cm). —H. Cross section of flower with guide rails (gr), corpusculum (cp), and style head (st). Scale bars = 1 mm (A), 100 μ m (H), 200 μ m (F), 300 μ m (B–E, G).

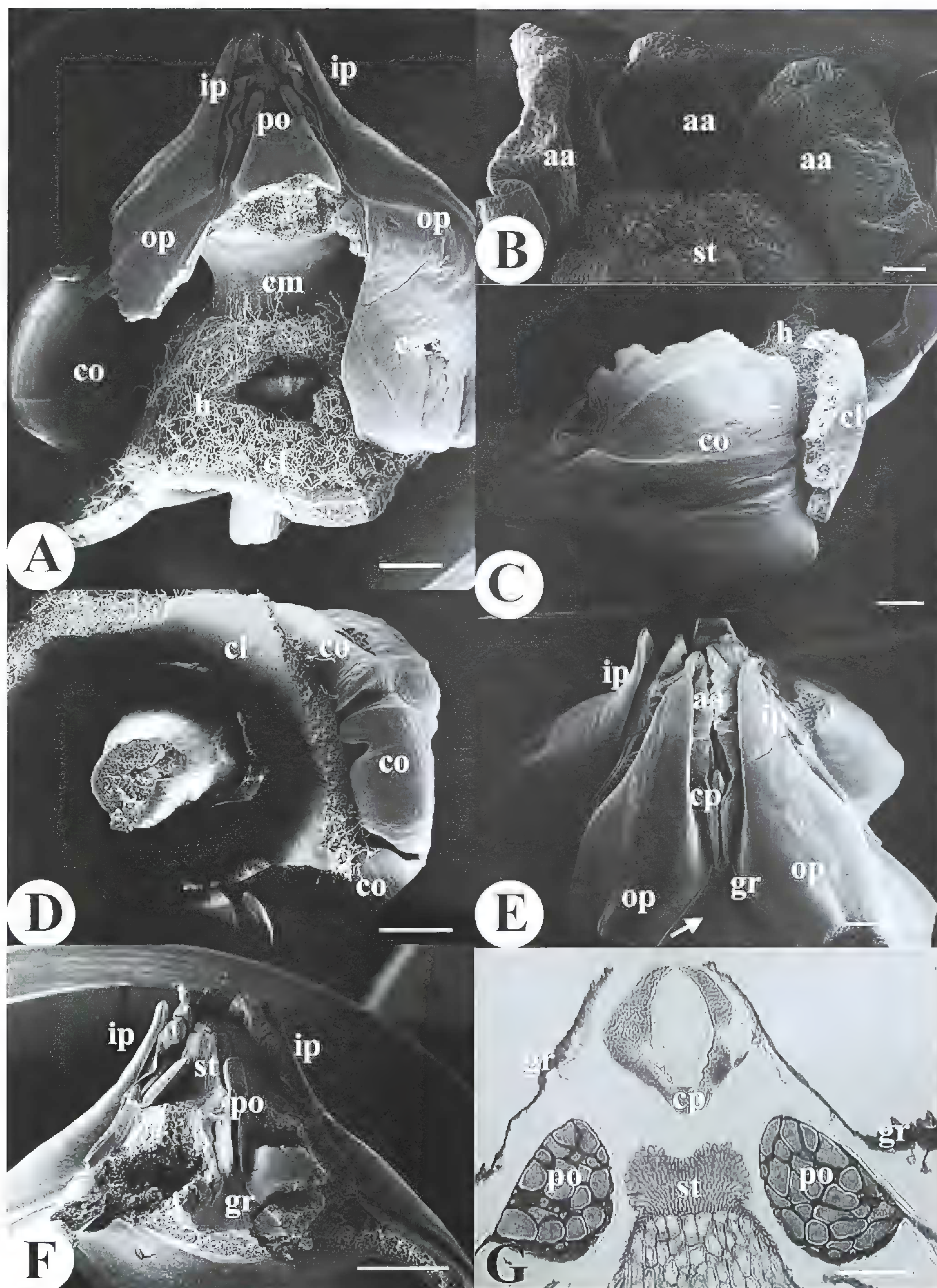


Figure 8. *Hoya inflata*. —A. Flower showing the remainder of the corolla (cl) with hairs (h), corona (co) with inner (ip) and outer (op) corona (co) processes, column (cm), and pollinia (po). —B. Upper part of flowers with anther appendages (aa) and style head (st). —C. Flower seen from side with corona (co) and the rest of corolla (cl) with hairs (h). —D. Flower seen from below with the remainder of the corolla (cl) and corona processes bent inward. —E–G. Upper part of flowers showing inner (ip) and outer (op) corona processes, guide rails (gr), anther appendages (aa), pollinia (po), style head (st), and corpuscula (cp). Arrow in E shows the fused processes of the corona. Scale bars = 1 mm (A, C–F), 100 mm (B, G).

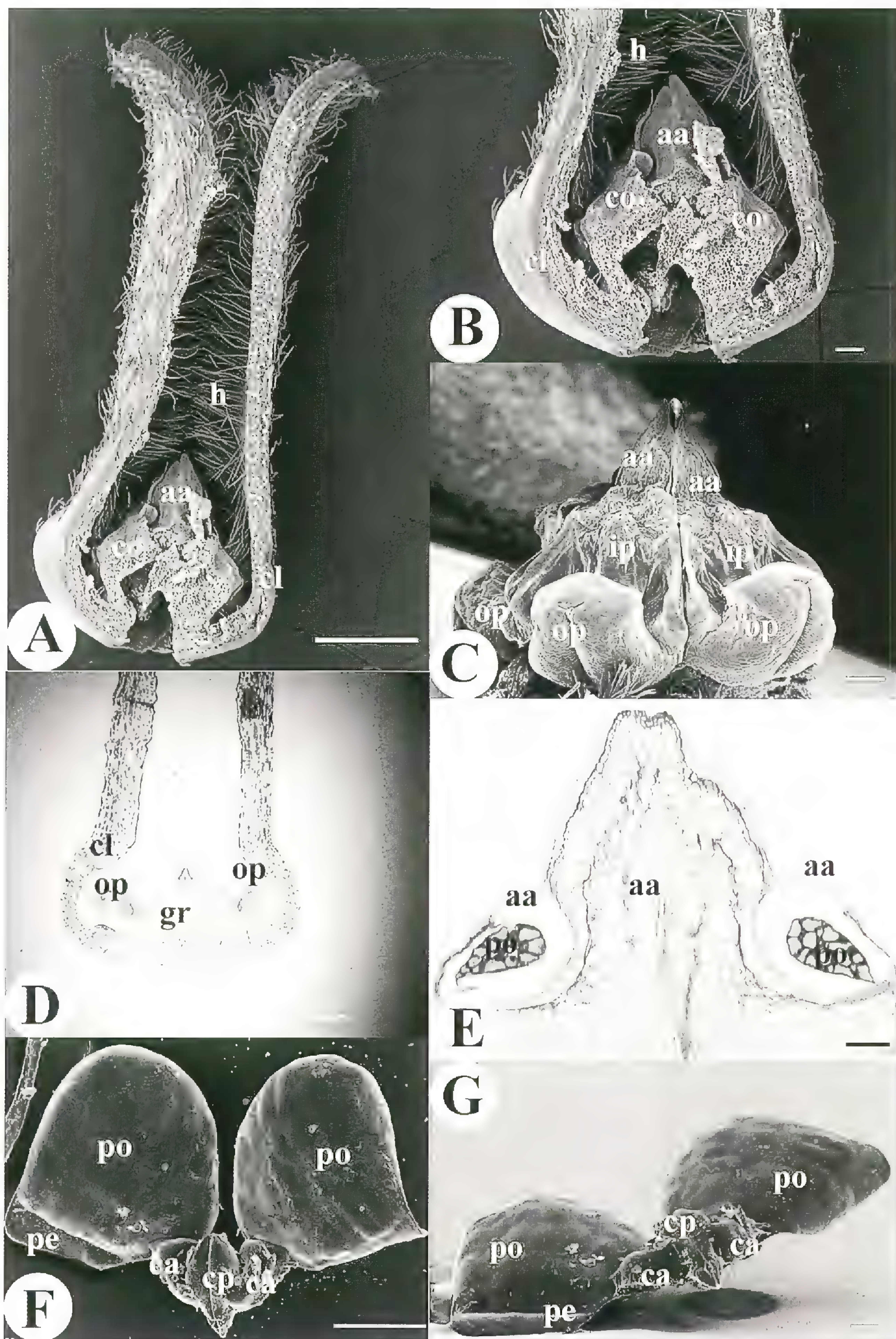


Figure 9. *Hoya yuennanensis*. —A, B, D. Longitudinally sectioned flowers with corolla (cl) with hairs (h), corona (co) with revolute outer processes (op), guide rails (gr), and anther appendages (aa). —C, E. Upper part of flower with inner corona processes (ip), revolute outer processes (op), anther appendages (aa), and pollinia (po). —F, G. Pollinaria with corpusculum (cp), caudicles (ca), and pollinia (po) with pellucid margins (pe). Scale bars = 1 mm (A), 1 mm (D), 30 μ m (G), 100 μ m (E, F), 200 μ m (B, C).

0.1 × 0.08 mm, ending with 2 short and straight appendages (Fig. 9F, G). Caudicles ca. 0.1 × 0.1 mm (Fig. 9F, G).

- 8. *Hoya patella*** Schltr., Bot. Jahrb. Syst. 50: 132. 1913. TYPE: New Guinea. *Schlechter 16375* (holotype, B not seen).

Hoya patella is an epiphyte with pendent or weakly twining stems and fleshy leaves from New Guinea. Inflorescences pedunculate, comprising racemes with 1 to 5 flowers; pedicels ca. 50 mm long, glabrous. Calyx lobes obtuse-triangular, ca. 2 × ca. 1 mm. Corolla campanulate, light pink, externally glabrous, hirsute, internally with reticulate nervature, ca. 3 cm diam.; lobes triangular-ovate, reflexed, ca. 5 × 2 mm, with hairy margins (Fig. 10A). Gynostegium on a short column (Fig. 10A). Corona much smaller than the corolla, dark red, smooth; inner processes slightly ascending (Fig. 10B), shorter than anther appendages (Fig. 10D, E); outer processes revolute but with margins that do not touch (Fig. 10C, G); anther appendages lanceolate, acute, exceeding the corona lobes (Fig. 10D, E); style head shortly apiculate (Fig. 10D, E, H). Pollinarium comprising 2 pollinia connected by short, flattened, winged caudicles to a corpusculum; pollinia longer than wide, cylindrical-elongate, protruding outward at the basal part, ca. 0.7 × 0.3 mm (Fig. 10F); pellucid margin covering the entire dorsal margin of the pollinia (Fig. 10F); corpusculum rhomboid, ca. 0.2 × 0.1 mm, ending with 2 short appendages (Fig. 10F); caudicles ca. 0.1 × 0.03 mm (Fig. 10F).

- 9. *Hoya retusa*** Dalzell, Kew J. Bot. 4: 294. 1852. *Hoya retusa* Warb. Repert. Spec. Nov. Regni Veg. 3: 344. 1907, nom. illeg. TYPE: Ind. Or. *Dalzell s.n.* (holotype, K not seen).

Hoya retusa is an epiphyte with non-twining pendent stems and fleshy foliage from India. Inflorescences pedunculate, comprising a much-reduced raceme carrying only a single flower; pedicels ca. 10 mm long. Calyx lobes elliptic-oblong, ca. 0.33 × 0.2 mm. Corolla flattened-campanulate, white, ca. 15 mm diam.; lobes triangular-acute, pubescent, ca. 5 × 2 mm. Corona outer processes keel-shaped, dark red; inner processes acutely ascending, outer processes deeply revolute (Fig. 11A–C, E); anther appendages lanceolate, acute, noticeably exceeding the corona lobes (Fig. 11B, C); style head shortly apiculate (Fig. 11A, D). Pollinarium comprising 2 pollinia connected by broadly flattened, unwinged caudicles to a corpusculum; pollinia oblong-elongate, ca. 0.4 × 0.2 mm (Fig. 11F); corpusculum ca. 0.3 ×

0.1 mm (Fig. 11F); caudicles ending with 2 short appendages, ca. 0.04 × 0.02 mm (Fig. 11F).

- 10. *Hoya venusta*** Schltr., Bot. Jahrb. Syst. 50: 128. 1913. TYPE: New Guinea. *Schlechter 18767* (holotype, B not seen).

Hoya venusta is an epiphytic climber with fleshy leaves from New Guinea. Inflorescences pedunculate, comprising umbels with 10 to 15 flowers, ca. 1.5 cm diam. Calyx lobes obtuse, 1–2.5 × 0.5 mm, glabrous. Corolla campanulate, white to dark pink, outside glabrous, internally papillose-hairy; lobes obovate, 5–7 × 5–6 mm. Gynostegium on a short column (Fig. 12A). Corona creamy white with light red center, striate; inner processes ascending, covering the style head (Fig. 12B–D), central part of the lobes with an umbo (Fig. 12B, F); outer processes deeply revolute (Fig. 12E); anther appendages lanceolate-acute, much exceeding the corona lobes (Fig. 12C, D); style head shortly apiculate (Fig. 12B–D). Pollinarium comprising 2 pollinia connected by broadly flattened, unwinged caudicles to a corpusculum; pollinia obovoid-oblong, ca. 0.4 × 0.2 mm (Fig. 12G, H); corpusculum small, rhomboid, size not measured (Fig. 12G, H); caudicles ca. 0.1 × 0.04 mm (Fig. 12G, H).

DISCUSSION

In his generic revision of the Marsdenieae, Omlor (1998) considered the genera *Absolmsia*, *Dischidia*, *Hoya*, *Madangia*, and *Micholitzia* to form a group (the *Hoya*-group) characterized by flowers having coronas with revolute outer processes, pollinia with pellucid margins, and fusiform seeds without prominent wings. Likewise, a close relationship between the genera *Hoya*, *Dischidia*, and *Micholitzia* has been reported in several molecular phylogenetic studies (e.g., Potgieter & Albert, 2001; Livshultz, 2002, 2003; Rapini et al., 2003; Meve & Liede, 2004). However, none of these studies resolved the phylogenetic relationship between these genera. In order to explore the boundaries of *Hoya*, Wanntorp et al. (2006a, b) analyzed 35 species of this genus and close relatives of the Marsdenieae. The monotypic genera *Absolmsia*, *Madangia*, and *Micholitzia* were found nested within *Hoya* with strong support (Wanntorp et al., 2006a, b).

Below, we discuss the position of *Absolmsia spartioides*, *Madangia inflata*, and *Micholitzia obcordata* nested within *Hoya* by comparing their flower morphology with that of closely related species of *Hoya*.

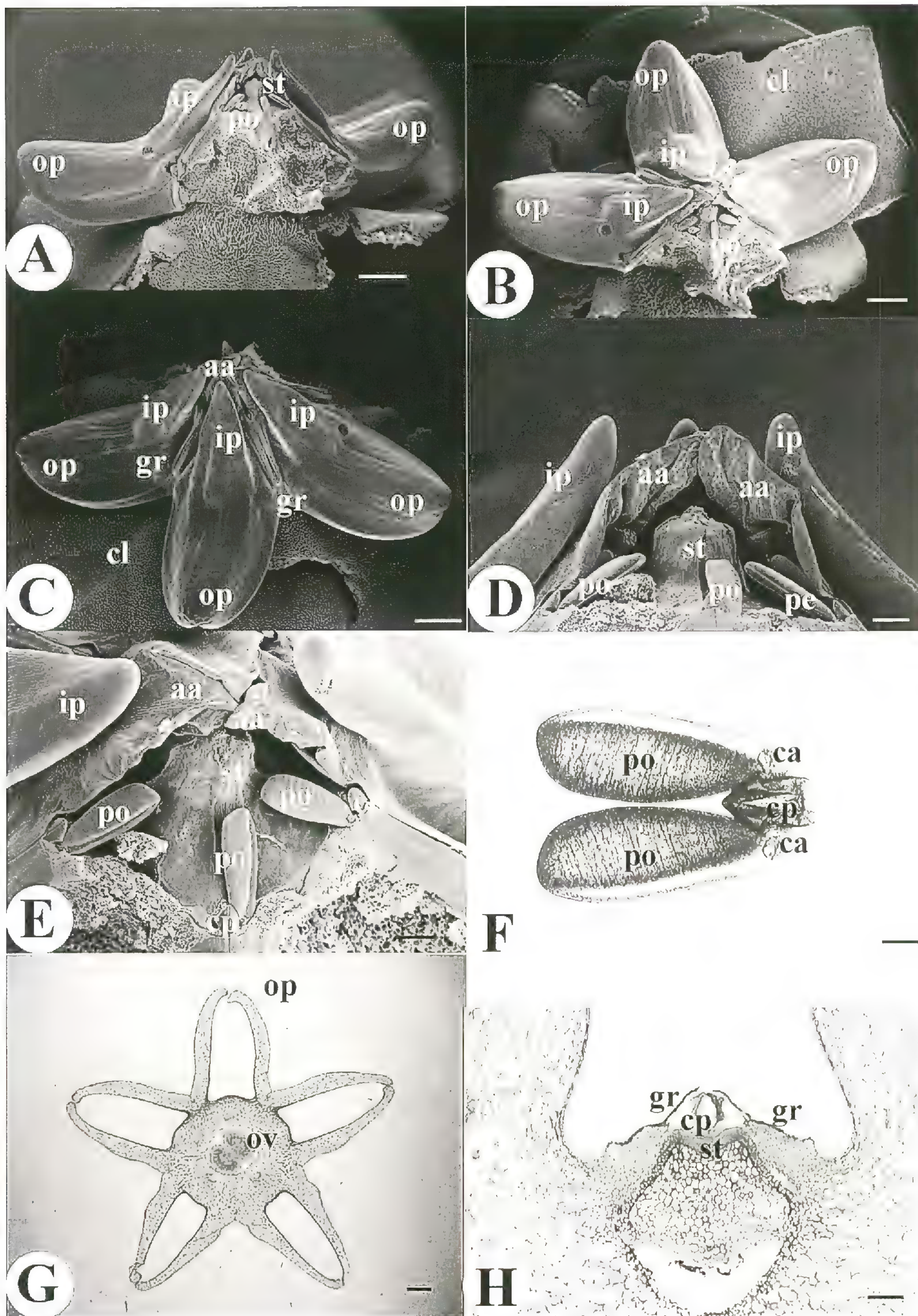


Figure 10. *Hoya patella*. — A–C. Side (A) and above (B, C) views of flowers with corolla (cl), corona with revolute outer processes (op), inner processes (ip), anther appendages (aa), guide rails (gr), pollinia (po), and style head (st). —D, E. Upper part of flower with inner (ip) corona processes, anther appendages (aa), pollinia (po) with pellucid margins (pe), corpusculum (cp), and style head (st). —F. Pollinarium with pollinia (po), corpusculum (cp), and caudicles (ca). —G. Cross section of lower part of flower showing ovary (ov) and outer corona (op) processes. —H. Longitudinal section of flower showing position of guide rails (gr), corpuscula (cp), and style head (st). Scale bars = 1 mm (A–C), 1.5 mm (G), 100 μ m (F, H), 200 μ m (D, E).

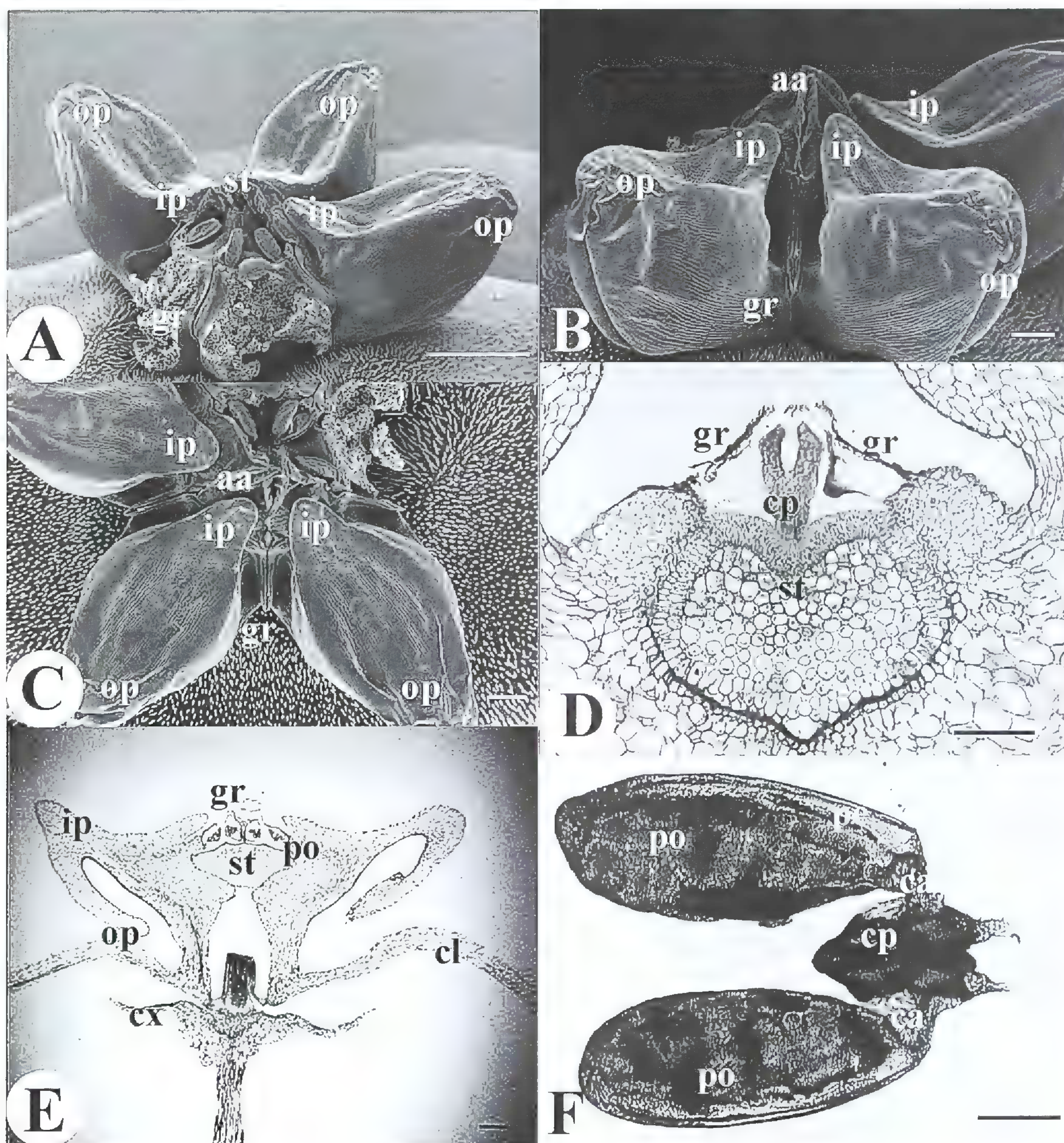


Figure 11. *Hoya retusa*. —A. Sectioned flower showing inner (ip) and outer (op) revolute corona processes, guide rails (gr), and style head (st). —B. C. Corona seen from side (B) and from above (C) showing inner (ip) and outer (op) revolute corona processes, guide rails (gr), and anther appendages (aa). —D. Longitudinal section of upper part of flower with guide rails (gr), corpusculum (cp), and style head (st). —E. Longitudinal section of flower showing calyx (cx), corolla (cl), inner (ip) and outer (op) corona processes, guide rails (gr), style head (st), and pollinia (po). —F. Pollinarium with pollinia (po), pellucid margins (pe), corpusculum (cp), and caudicles (ca). Scale bars = 1 mm (A), 3 mm (B), 100 μ m (D, F), 300 μ m (C, E).

THE GENERIC STATUS OF *ABSOLMSIA*

At first sight, mature plants of *Absolmsia* look very unlike *Hoya* because they lack the leaves characteristic of that genus. Leaves are only present in very young plants of *Absolmsia*; in mature plants, photosynthesis is instead carried out mainly by long, green, perennial peduncles of the inflorescences. In most species of *Hoya*, the peduncles are also perennial; only a few *Hoya* species have annual peduncles, a derived character state in this genus and

almost entirely found in the section *Eriostemma* Schltr.

Absolmsia spartioides was first described by Benth. in 1880 as *Astrostemma spartioides* Benth., but this name was later changed to *Absolmsia* by Kuntze, because he regarded it as too similar to the name of another genus of tribe Marsdenieae, *Asterostemma* Decne. (Omlor, 1998). The similarity between *Absolmsia* and *Hoya* was first pointed out by Schlechter (1916: 2), who stated that “*Absolmsia*, placed by K. Schumann within Cynanchinae, belongs

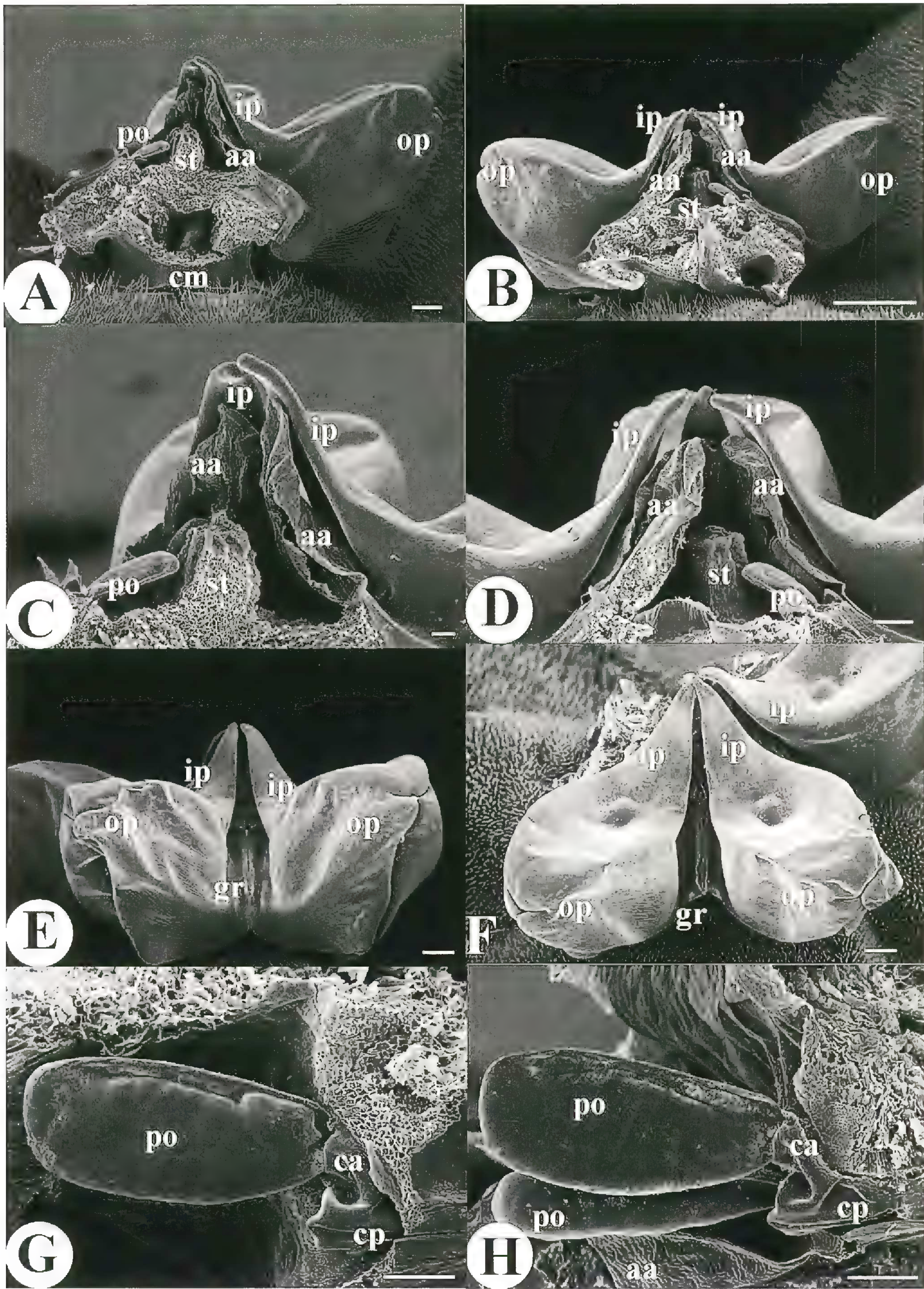


Figure 12. *Hoya venusta*. —A–D. Details of flowers showing the corona with inner (ip) and outer (op) revolute processes, column (cm), anther appendages (aa), style head (st), and pollinia (po). —E, F. Coronas seen from side showing guide rails (gr). —G, H. Pollinaria adnate to anther appendage (aa), with pollinia (po), corpuscula (cp), and caudicles (ca). Scale bars = 1 mm (B), 100 μ m (C, G, H), 200 μ m (D), 300 μ m (A, E, F).

without any doubts near to *Hoya*.” Omlor (1998) included *Absolmsia* in a *Hoya*-group based on several morphological characters common to both of these genera: a corona with inner processes that cover the anthers and outer revolute processes (Fig. 1D, E); pollinia with a dorsal pellucid margin (Fig. 2H); and almost round seeds with thickenings on the lateral walls of cells in their seed coats. Based on morphological similarities in the shapes of the corona and corolla, Kloppenburg reduced *Absolmsia* to synonymy under *Hoya*, transferring the name as *H. spartioides* (Kloppenburg, 2001).

The available molecular phylogeny for *Hoya* indicates that the sister group of *Absolmsia spartioides* is *H. curtisii* and that these two species are part of a weakly supported clade also including *H. lacunosa* and a well-supported subclade with *H. imbricata* and *H. caudata* (Wanntorp et al., 2006b). *Absolmsia spartioides* and *H. curtisii* differ substantially in flower morphology, the latter having a corolla with completely reflexed lobes and a corona lying on an annulus (Fig. 4A, B), while *Absolmsia* has a campanulate corolla and a corona without any annular structure (Fig. 1A, C). Because the sample of *Hoya* species included in the molecular studies of Wanntorp et al. (2006a, b) was limited to only 35 out of over 300 species of *Hoya*, it is probable that the retrieved sister relationship between *A. spartioides* and *H. curtisii* will change by the inclusion of additional species of *Hoya* in the molecular phylogeny. Although it is not possible at this stage to point to a particular species of *Hoya* as sister to *Absolmsia*, the inclusion of this genus in *Hoya* was nevertheless clearly shown in the tree of Wanntorp et al. (2006a, b) and is in concordance with previous morphological studies (Omlor, 1998; Kloppenburg, 2001).

The shape of the corolla varies extensively in *Hoya* from rotate with revolute lobes (e.g., *H. lacunosa*, Fig. 7A), flattened-campanulate in *H. caudata* (Fig. 3A), or urceolate to globose in *H. heuschkeliana* Kloppenb. and *H. telosmoides* R. Omlor (Omlor, 1996). The corolla lobes are commonly reflexed as in *H. curtisii*. Corolla characters (especially the shape) in *Hoya* seem highly labile and have undoubtedly evolved numerous times. The shape of the corona, on the other hand, seems to be a character of higher phylogenetic value for linking *Absolmsia* to *Hoya*, as both have coronas with deeply revolute outer processes to the lobes (Omlor, 1998; Fig. 1D, E). In addition, the gynostegium of *Absolmsia*, as in many species of *Hoya*, is raised above the corolla on a column that varies in the degree of indument and in conspicuousness. This column is short in *Absolmsia* (Fig. 1C), *H. patella* (Fig. 10A), and *H. caudata* (Fig. 3B) and not as conspicuous as in *H. curtisii*

(Fig. 4D). Pollinia of *Absolmsia*, *Hoya*, *Micholitzia*, and *Madangia* have a pellucid dorsal margin in which pollen tubes germinate (Omlor, 1998; this study). This trait is unknown in the genus *Dischidia* (Meve, 2001) and all other species of the Marsdenieae (Omlor, 1998). These morphological characters and the molecular results (Wanntorp et al., 2006a, b) support the inclusion of *Absolmsia* in *Hoya*, transferred by Kloppenburg (2001) as *H. spartioides* (Benth.) Kloppenb.

THE GENERIC STATUS OF *MADANGIA*

Forster et al. (1997) collected a plant in the Madang province of New Guinea that very much resembled species of *Hoya* in its epiphytic habit and fleshy leaves. The plant was assigned to the monotypic genus *Madangia* on the basis of floral morphological characters unique for this species. One of these characters was the globose shape of the corolla, which is unusual in *Hoya* as discussed by Forster et al. (1997), who mentioned *H. heuschkeliana* as the only species with similar corolla shape. Omlor (1996) also mentioned a species from Sabah, *H. telosmoides*, with a similar corolla shape, although this species has corollas internally covered with long recurved hairs. *Madangia inflata* is well supported as sister species to the New Guinean *H. hypolasia*, both being part of a larger clade, including other species from Australia and New Guinea (e.g., *H. patella*, *H. venusta*, and a subclade with *H. australis* R. Br. ex J. Traill and *H. albiflora* Zipp. ex Blume) (Wanntorp et al., 2006a, b). *Hoya heuschkeliana*, on the other hand, was associated with species from the *Acanthostemma* Blume group, which have pubescent corollas and completely reflexed lobes that give the flowers a globular shape. *Hoya telosmoides* was not found close to *M. inflata* in the tree (Wanntorp et al., 2006b). These results again support the plasticity of the corolla in *Hoya* and underline the hazard of establishing too much reliance upon single corolla characters in the recognition of genera in the group.

The corona of *Madangia inflata* has a remarkable shape, which contributed to the decision of Forster et al. (1997) to establish a new genus for this species. The five inner corona processes are free at the apical part near the style head as in *Hoya*, but their outer parts, corresponding to the outer processes of the corona lobes in *Hoya*, form a continuous rim that is folded inward (Fig. 8D). A similar corona shape, which has not been previously discussed, is found in *H. lacunosa* (Fig. 7B). In this species also, the five outer corona lobes are fused at their basal part, forming a skirt that somewhat resembles the membranous corona of *Madangia* (Fig. 8D). According to

Wanntorp et al. (2006b), *H. lacunosa*, however, groups with many other species of *Hoya* and is clearly separated from *M. inflata*. This corona type therefore seems to have arisen independently several times in *Hoya*, paralleling the variation in corolla morphology.

The remaining flower parts of *Madangia* are very similar to *Hoya*. The column between the corolla and the gynostegium is very conspicuous in *Madangia* as in many species of *Hoya*, such as *H. curtisii*, *H. lacunosa*, and *H. venusta* (Figs. 4D, 7G, 12A). The pollinia of *Madangia* (Fig. 2C, D) have a clear pellucid margin as in *Hoya* (e.g., Fig. 6G). Another interesting character not previously noted in *Madangia* is the dimerous style head that is flat and shortly apiculate in both *Madangia* and *H. hypolasia* (Figs. 8B, 6C) and shortly apiculate-conical in *H. macgillivrayi* F. M. Bailey, *H. venusta* (Fig. 12C, D), and *H. patella* (Fig. 10D) of the same clade. The shape of the style head and the morphology of the pollinaria are in agreement with the molecular results of Wanntorp et al. (2006b), and we propose that *Madangia* should be included in *Hoya* as *H. inflata*.

THE GENERIC STATUS OF *MICHOLITZIA*

During an expedition to India and Burma, the orchid collector W. Micholitz discovered a new taxon, later described as *Micholitzia obcordata* (Brown, 1909). *Micholitzia* was again collected in China by Handel-Mazzetti and in India by Deb and named, respectively, *H. yuennanensis* Hand.-Mazz. and *H. manipurensis* Deb. In 1974, Tsiang and Li collected the same plant in China, thought it to be a new species of *Hoya* that they called *H. lantsangensis* Tsiang & P. T. Li, and erected a new section *Antiostelma* for it. Maxwell transferred *Micholitzia* to *Dischidia* (1991), and P. T. Li (1992: 218) argued that the cylindric shape of the corollas and the bud aestivation, which “twisted leftward,” were different enough from those of *Hoya* and *Dischidia*, with valvate aestivation and rotate and urceolate corollas, respectively, to raise section *Antiostelma* in *Hoya* to generic rank. According to molecular evidence (Wanntorp et al., 2006a), *Micholitzia* is nested within *Hoya*, even though its sister relationship to any of the species of *Hoya* is less clear. In habit, *Micholitzia* is more similar to *Absolmsia* than to *Hoya*, *Dischidia*, or *Madangia*. In these last three genera, but not in *Micholitzia* and *Absolmsia*, adventitious roots are produced at the leaf nodes (Goyder & Kent, 1994). The corolla of *Micholitzia* is of a similar urceolate or tubular shape to that of a few species of *Hoya* (e.g., *H. heuschkeliana*) but is wider at the lower part of the corollas (Goyder & Kent, 1994). This shape superficially resembles that of many species of *Dischidia*, but in this genus usually

only the upper internal part of the corolla is pubescent, while in *Micholitzia* the corollas are uniformly pubescent on the outside and inside (Goyder & Kent, 1994). The corona of *Micholitzia* has been considered to be different from that of *Dischidia* and *Hoya* because its five fleshy and almost round lobes do not end as in *Hoya* with five pointed inner processes on the anther appendages. Its inner corona processes are instead blunt-ended and appear almost as if they were united to the five conspicuous anther appendages hiding the flat and short style head. Despite the different inner corona processes of *Micholitzia*, the outer processes of the corona lobes have revolute margins (Fig. 9C) similar to those of *Hoya* (e.g., *H. retusa*) (Omlor, 1998; Fig. 11B). In addition, the pollinaria of *Micholitzia* have clear pellucid margins (Omlor, 1998; Fig. 9F). Clear pellucid margins are also present in *Absolmsia* (Fig. 2H), *Madangia* (Fig. 2C), and *Hoya* (e.g., Fig. 5E) but are absent in *Dischidia*. The position of the pellucid margin of *Micholitzia*, however, is superficially different from *Hoya* because it is apparently situated at the lower part of the pollinia instead of at the outer edge (Fig. 9F), but as observed by Goyder and Kent (1994), this is due to the twisting of the pollinia of *Micholitzia*. By rotating the pollinia at 90°, the pellucid margin takes the same position as in the pollinia of *Hoya*. Based on the molecular evidence for *Hoya* and on the similarity of the pollinia and of the outer corona processes, *Micholitzia* should be included in a broadly defined *Hoya*. Due to the prior use of the epithet *obcordata* in *Hoya*, inclusion of *Micholitzia obcordata* in *Hoya* necessitates a change of epithet for the species, based on the next available name of the several synonymous species, which is *H. yuennanensis*.

CONCLUSION

A recurring theme in recent molecular-based phylogenies within the Apocynaceae, Asclepiadoideae is that morphological classifications based on single, albeit unusual, floral features (especially of the corolla or coronas) are not corroborated by molecular data (e.g., Meve & Liede, 2001, 2002, 2004). In the *Hoya* group, the molecular phylogeny to date (Wanntorp et al., 2006b) indicates relationships that follow geographical patterns, as shown by the clade including almost exclusively Australian and New Guinean species, but also partly reflect morphological similarity, as in *Madangia*, *Absolmsia*, and *Micholitzia*.

Literature Cited

- Bentham, G. 1868. Asclepiadaceae. Pp. 324–348 in G. Bentham & F. Mueller (editors), *Flora Australiensis*, Vol. 4. Lovell Reeve & Co., London.

- Brown, N. E. 1909. *Micholitzia* N. E. Br. Bull. Misc. Inform. Kew 1909: 358–359.
- Deb, D. B. 1955. A new species of *Hoya* from Manipur. J. Indian Bot. Soc. 34: 50–52.
- Endress, M. E. & P. V. Bruyns. 2000. A revised classification of the Apocynaceae s.l. Bot. Rev. 66: 1–56.
- & W. D. Stevens. 2001. The renaissance of the Apocynaceae s.l.: Recent advances in systematics, phylogeny, and evolution: Introduction. Ann. Missouri Bot. Gard. 88: 517–522.
- Forster, P. I. 1995. Circumscription of *Marsdenia* (Asclepiadaceae: Marsdenieae), with a revision of the genus in Australia and Papuasia. Austral. Syst. Bot. 8: 703–933.
- & D. J. Liddle. 1996. *Hoya*. Pp. 231–237 in A. E. Orchard (editor). Flora of Australia 28. CSIRO, Melbourne.
- , ——— & I. M. Liddle. 1997. *Madangia inflata* (Asclepiadaceae: Marsdenieae), a new genus and species from Papua New Guinea. Austrobaileya 5: 53–57.
- , ——— & ———. 1998. Diversity in the genus *Hoya* (Asclepiadaceae–Marsdenieae). Aloe 35: 44–48.
- , ——— & ———. 1999. The genus *Hoya* R. Br. (Asclepiadaceae: Marsdenieae) as commonly cultivated in Australia. Asklepios 78: 18–32.
- , ——— & ———. 2002. *Dischidia*, *Hoya* (Asclepiadaceae). Pp. 90–103 in R. Spencer (editor). Horticultural Flora of South-eastern Australia, Vol. 4. Univ. New South Wales Press, Sydney.
- Gilbert, M. G., W. D. Stevens & P.-T. Li. 1995. Notes on the Asclepiadaceae of China. Novon 5: 1–16.
- Goyder, D. J. & D. H. Kent. 1994. *Micholitzia obcordata* N. E. Br. : (Asclepiadaceae, Marsdenieae) reinstated. Asklepios 62: 13–20.
- Holmgren, P. K., N. H. Holmgren & L. C. Barnett. 1990. Index Herbariorum 1: The Herbaria of the World. New York Botanical Garden, New York.
- Igersheim, A. & O. Cichocki. 1996. A simple method for microtome sectioning of prehistoric charcoal specimens, embedded in 2-hydroxymethyl methacrylate (HEMA). Rev. Palaeobot. Palynol. 92: 389–399.
- Kleijn, D. & R. van Donkelaar. 2001. Notes on the taxonomy and ecology of the genus *Hoya* (Asclepiadaceae) in Central Sulawesi. Blumea 46: 457–483.
- Kloppenburg, D. 2001. Change of genus. Fraterna 14: 8–10.
- Li, P.-T. 1992. *Antiostelma* (Asclepiadaceae), a new genus from China. Novon 2: 218–219.
- Liede, S. & F. Albers. 1994. Tribal disposition of Asclepiadaceae genera. Taxon 43: 201–231.
- Livshultz, T. 2002. Systematics and evolution of ant-leaves in the genus *Dischidia* (Asclepiadaceae). ASPT annual meeting, Portland, Oregon, Botany 2000. Abstract No. 94.
- . 2003. Lectotypification of *Dolichostegia* Schlechter (Asclepiadoideae, Apocynaceae) and a new combination, *Dischidia boholensis*. Taxon 52: 595–600.
- Maxwell, J. F. 1991. Botanical notes on the vascular flora of Chiang Mai Province, Thailand: 2. Nat. Hist. Bull. Siam Soc. 39: 71–83.
- Meve, U. 2001. *Hoya heuschkeliana*, a neo-endemic of Mt. Balusan (Philippines, Luzon), and remarks on the urceolate flower type in Asclepiadoideae. Asklepios 82: 7–10.
- & S. Liede. 2001. Inclusion of *Tenaris* and *Macropetalum* in *Brachystelma* (Apocynaceae–Asclepiadoideae–Ceropegieae) inferred from non-coding nuclear and chloroplast DNA sequences. Pl. Syst. Evol. 228: 89–105.
- & ———. 2002. A molecular phylogeny and generic rearrangement of the stapelioid Ceropegieae (Apocynaceae–Asclepiadoideae). Pl. Syst. Evol. 234: 171–209.
- & ———. 2004. Subtribal division of Ceropegieae. Taxon 53: 61–72.
- Omlor, R. 1996. Notes on Marsdenieae (Asclepiadaceae): A new, unusual species of *Hoya* from northern Borneo. Novon 6: 288–294.
- . 1998. Generische Revision der Marsdenieae (Asclepiadaceae). Doctoral dissertation. Shaker Verlag, Aachen.
- Potgieter, K. & V. Albert. 2001. Phylogenetic relationships within Apocynaceae s. l. based on *trnL* intron and *trnL-F* spacer sequences and propagule characters. Ann. Missouri Bot. Gard. 88: 523–549.
- Rapini, A., M. W. Chase, D. J. Goyder & J. Griffiths. 2003. Asclepiadeae classification: Evaluating the phylogenetic relationships of New World Asclepiadoideae (Apocynaceae). Taxon 52: 33–50.
- Schlechter, R. 1916. Neue Asclepiadaceen von Sumatra und Celebes. Beih. Bot. Centralbl. 34: 1–18.
- Sennblad, B. & B. Bremer. 2002. Classification of Apocynaceae s.l. according to a new approach combining Linnaean and phylogenetic taxonomy. Syst. Biol. 51: 389–409.
- Tsiang, Y. & P.-T. Li. 1974. Praecursores florae asclepiadacearum sinensium. Acta Phytotax. Sin. 12: 79–149.
- Verhoeven, R. L., S. Liede & M. Endress. 2003. The tribal position of *Fockea* and *Cibirhiza* (Apocynaceae: Asclepiadoideae): Evidence from the pollinium structure and cpDNA sequence data. Grana 42: 70–81.
- Wanntorp, L., A. Kocyan, R. van Donkelaar & S. S. Renner. 2006a. Towards a monophyletic *Hoya* (Marsdenieae, Apocynaceae): Inferences from the chloroplast *trnL* region and the *rbcl-atpB* spacer. Syst. Bot. 31: 586–596.
- , ——— & S. S. Renner. 2006b. Wax plants disentangled: A phylogeny of *Hoya* (Apocynaceae) using molecular markers. Molec. Phylog. Evol. 39: 722–733.